

BIOGEOGRAPHIC PATTERN OF PHYLOGENY IN A CLADE
OF ENDEMIC HAWAIIAN SPIDERS (ARANEAE, TETRAGNATHIDAE)

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The biota of the Hawaiian archipelago offers an ideal system with which to study the dynamics behind the evolutionary process, both because the islands harbour many speciose lineages, and because they are arranged within a chronological time frame. Over the past 5 years I have begun to uncover an unexplored radiation of one of Hawaii's most abundant and conspicuous invertebrate groups: the spider genus *Tetragnatha*. The current study focuses on a small clade within the lineage, in which all the component species have abandoned web-building, instead foraging as cursorial predators. I examine 2 primary questions: 1. What has been the relative importance of strict geographic isolation (populations on different volcanoes) versus divergence between contiguous habitats (populations on the same volcano) in the evolution of this clade? 2. Does the phylogeny indicate a pattern of ecological and distributional change which could suggest that ecological rather than sexual shifts may underlie species formation? I generated a phylogeny based on morphological characters, and compared this phylogeny to the biogeographic pattern of the Hawaiian Islands. The results suggest that, for this clade of cursorial species, speciation requires strict geographic isolation, and ecological (more than sexual) shifts appear to play a role in initiating divergence. Considering the islands as a series of evolutionary snapshots, I would also speculate that speciation is commencing on the youngest island (Hawaii), and developing on the adjacent older island of Maui. □ *Tetragnatha*, phylogeny, Hawaii, speciation, allopatry.

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Species represent one of the basic units of evolution, yet the processes by which they are formed remain poorly understood (Mayr, 1963). Studies of the Hawaiian biota have lent considerable insight into the mechanisms underlying speciation. These studies are highlighted by the Hawaiian *Drosophila*, in which sexual selection through female choice appears to play an integral role in inducing species formation among small populations colonizing geographically isolated islands (Carson, 1968; Carson and Kaneshiro, 1976; Kaneshiro, 1988). One may ask whether it is possible to generalize from these studies that adjustments in the sexual environment are largely responsible for driving species radiations. Other studies outside the Hawaiian Islands have found that ecological changes in isolation are more important in driving species proliferation (Mayr, 1963; Grant, 1986). When a species is released from interaction with related species, by whatever means, it may broaden its habitat use and exhibit much more variation among individuals (Lack, 1971; McCune, 1990). The argument is that if such a reproductively isolated incipient species were reunited with its parent, selection could act on the ecological variability

to minimize the resources jointly used by both species, leading to further ecological divergence (Mayr, 1963; Grant, 1986).

The Hawaiian archipelago (Fig. 1) provides a natural laboratory for studies of speciation (Simon, 1987). First, the extreme isolation of the islands has allowed repeated and explosive diversification of species in a large number of lineages including honeycreepers (Berger, 1981; Freed et al., 1987), land snails (Cooke et al., 1960), crickets (Otte, 1989) and drosophilid flies (Kaneshiro and Boake, 1987). Further, the islands are a series of volcanoes arranged within an identifiable chronological time frame; the currently high islands range from Kauai, the oldest and most eroded, to Hawaii, the youngest, highest and largest, with 5 separate volcanoes.

This study uses a lineage of spiders to examine speciation patterns within the context of the Hawaiian archipelago. The spiders belong to the long-jawed orb-weaving genus *Tetragnatha*, which comprises a large number of endemic species in the Hawaiian Islands (Gillespie, 1991, 1992). Outside the archipelago, *Tetragnatha* are among the most widespread and conspicuous spiders worldwide, yet collectively they are also

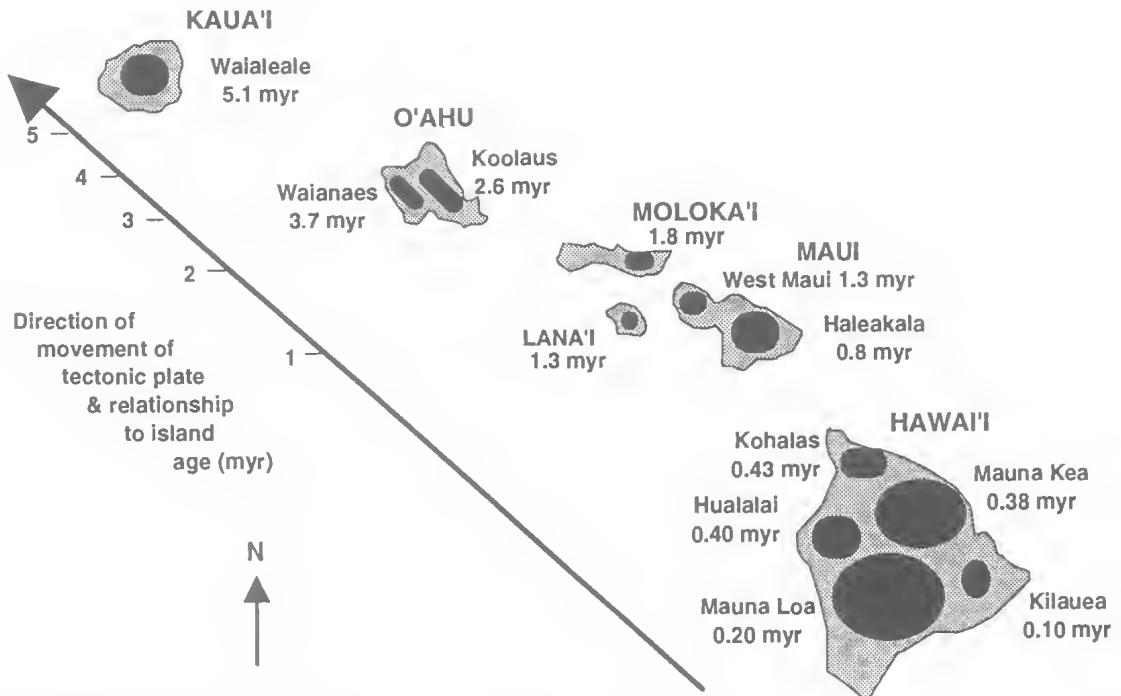


FIG. 1. Major land masses of the Hawaiian archipelago, indicating approximate age, and direction of movement of tectonic plate.

one of the most homogeneous, both in morphology (elongate bodies and long legs) and ecology (orb web generally built over or near water) (Wiehle, 1963; Levi, 1981; Gillespie, 1986, 1987). Hawaiian species of *Tetragnatha* represent a paradox, exhibiting considerable morphological and ecological diversity. Until 1992, the sole reference to endemic Hawaiian representatives of the genus was based on descriptions of a single species by Karsch (1880) and 8 species by Simon (1900, redescribed by Okuma, 1988). I have now described an additional 16 species (Gillespie, 1991, 1992), and have collected more than 60 new taxa that span a broad spectrum of colours, shapes, sizes, ecological affinities, and behaviours. In terms of courtship behaviour, however, Hawaiian representatives of the genus display the simple cheliceral locking mechanism characteristic of the genus (Levi, 1981; Gillespie, pers. obs.).

Here I examine a small clade (the 'spiny-leg' clade) within the radiation of Hawaiian *Tetragnatha*. Representatives of this clade are characterized by a cursorial habit, and do not build webs (Gillespie, 1991). Further, in common with other representatives of the genus (Levi, 1981), but in striking contrast to the *Drosophila* radiation, these spiders display minimal courtship be-

haviour. Because explanations for species formation in the Hawaiian *Drosophila* rely heavily on the elaborate courtship behaviour of the group, the absence of such behaviour in the Hawaiian *Tetragnatha* suggests that alternative explanations might be required to account for species proliferation. The questions I address in this study are: 1. What has been the relative importance of strict geographic isolation (taxa diverge on different volcanoes) versus divergence between contiguous habitats (taxa diverge on the same volcano) in the evolution of the spiny-leg clade of Hawaiian *Tetragnatha*? I generated a phylogeny for the clade based on morphological characters, and then compared the phylogeny to the biogeographic pattern and history of the islands. 2. Does the phylogeny indicate a pattern of ecological and distributional change which could suggest that ecological rather than sexual shifts may underlie species formation?

METHODS

COLLECTION AND ECOLOGICAL MEASUREMENTS

Spiders were collected by visual night searching at various times of the year between 1987 and 1991 in wet, mesic and dry native forest in all of the currently high Hawaiian Islands (Kauai,

Oahu, Molokai, Lanai, Maui and Hawaii; Fig. 1). Habitats from which spiders were taken were scored as wet (>450cm average annual rainfall), mesic (250-450cm) or dry (<250 cm). Elevation was categorized as low (<1000 m), medium-low (1000-1700m), medium-high (1700-2000m) and high (>2000m). Microhabitat associations were determined by categorizing the specific site from which an individual was collected (roots, fern fronds, against bark, etc.) (Gillespie, 1987).

PHYLOGENETIC ANALYSIS

I used a cladistic approach (Hennig, 1966) based on morphological characters to determine relationships among the spiny-leg clade of Hawaiian *Tetragnatha*. I scored a total of 30 characters relating to cheliceral armature (upper and lower tooth rows), leg spination, and colour of the cephalothorax and abdomen (Table 1). In addition, I scored characters from the detailed structure of the male palp using a Hitachi S-800 scanning electron microscope. I used a Hawaiian web-building species of *Tetragnatha*, *T. stelarobusta* Gillespie as an outgroup in the analysis because molecular data indicate that this species belongs to a closely related sister clade of the spiny-leg species (H.B. Croom, pers. comm.).

Characters were analyzed as unordered states (i.e., any character state permitted to transform directly into any other state) using Fitch (Fitch, 1971) and Wagner (Farris, 1970) parsimony in PAUP (Swofford, 1990) under the accelerated transformation method of optimization. Character states were polarized as primitive or derived by outgroup comparison (Maddison *et al.*, 1984), and characters were scaled for equal character weighting regardless of the number of states. A branch-and-bound search was conducted to find the shortest tree. The data were then reanalyzed by successive approximations, weighting characters according to their rescaled consistency index (Farris, 1969, 1989).

RELATIONSHIP BETWEEN SPECIES PHYLOGENY AND ISLAND BIOGEOGRAPHY

To test the importance of strict geographic isolation in initiating divergence, and the extent to which regular ecological and distributional changes have accompanied species formation, I compared the resulting phylogeny to the biogeographic locations of the component taxa within the Hawaiian archipelago.

RESULTS

COLLECTION AND ECOLOGICAL MEASUREMENTS

Representatives of the spiny-leg clade of Hawaiian *Tetragnatha* occur on each of the high islands. All are restricted to wet forest except for *T. brevignatha* Gillespie, *T. restricta* Simon and *T. quasimodo* Gillespie, which occur in wet, mesic, and sometimes dry, forest. The ranges over which the different species were found is listed in table 2. Microhabitat associations were loose, although the bright green species (*T. tantalus* Gillespie, *T. polychromata* Gillespie, *T. brevignatha*, *T. macracantha* Gillespie, *T. waikamoi* Gillespie and *T. kawaiensis*) were collected almost entirely from leaves, whereas the darker coloured *T. kamakou* Gillespie, *T. perreirai* Gillespie, *T. pilosa* Gillespie, *T. quasimodo* and *T. restricta* were collected from brown or red-brown substrates.

PHYLOGENETIC ANALYSIS

When characters were scaled for equal weighting regardless of number of states and unordered, a total of 7 most parsimonious trees were generated (consistency index 0.517, retention index 0.509). Subsequent weighting by successive approximations had little effect on the tree topology, and gave a single tree of unweighted length 76 (consistency index 0.725, retention index 0.765). Fig. 2 shows the tree with explanations of the characters defining each node. The characters defining species are marked as bars.

RELATIONSHIP BETWEEN SPECIES PHYLOGENY AND ISLAND BIOGEOGRAPHY

As can be seen from this phylogeny based on morphological characters (Fig. 2), the most closely related species are never found on the same island. The only regular pattern of ecological and distributional change through the Hawaiian Islands is the broadening habitat usage on the younger islands. In particular, taxa on the oldest islands (Kauai and Oahu) are all endemic to single volcanoes, while on the youngest island, Hawaii, there are no species endemic to the island, despite its much larger size (5 volcanoes). In addition, taxa on the youngest island occupy a much broader range of habitat types: *T. brevignatha*, for example, is found at all elevations and in dry, mesic and wet forest on Hawaii Island, whereas representatives of this species on East Maui occur only in mesic forest at middle elevations. Distributions of representatives of the clade on East Maui show some anomalies. In particular,

		stel	kau	pil	mac	pol	tant	wak	brev	perr	kam	rest	quas
1	♀ first tooth: tiny/moderate size/as large as others	1	1	1	1	1	1	2	1	1	1	1	0
2	♂ first tooth: absent /bump/linger	2	2	2	0	1	1	2	0	2	2	2	2
3	♂ 'sl' (first tooth down margin): bent up/straight/bent down	1	1	1	1	1	0	1	0	1	1	1	2
4	♂ 'sl' close to '1' (second tooth down margin)?	0	0	0	0	0	0	0	0	0	1	1	1
5	♂ apical tooth (lower chelicera) present?	1	1	0	0	0	1	1	0	1	0	0	0
6	No. large teeth on lower margin ♂ chelicera: 1/2	0	1	0	1	1	1	1	0	1	1	0	1
7	♂ lower tooth row: short/ long	1	1	0	1	1	1	1	0	0	1	0	1
8	♂ teeth 3 and 4 on lower margin much smaller than rest?	1	1	1	0	1	1	1	1	0	1	1	1
9	♂ teeth 5 onwards larger than 3 and 4?	1	1	1	0	1	1	1	1	1	1	1	1
10	♂ first two teeth well separated?	1	0	1	1	1	1	0	0	0	0	0	0
11	Curl on terminal projection, conductor: none/ slight/ complete	0	1	1	1	0	2	2	1	1	1	2	0
12	Terminal projection of conductor points: straight/ backward/ forward	0	2	2	2	0	2	2	2	2	2	2	1
13	Cap of conductor tip: shallow/ deep	0	0	1	1	0	0	0	0	1	1	1	0
14	Cap ridge of conductor tip: lateral/ medial	0	0	0	0	0	1	1	0	1	0	0	0
15	Backward projection of conductor tip: above/ at same level/ below cap	0	0	0	1	1	0	0	0	1	1	1	1
16	Spur of conductor tip: indistinct/ prominent	0	1	1	1	1	1	1	1	1	1	1	1
17	Spur of conductor tip: angled up/ straight out/ hooked down	1	2	0	2	1	1	1	0	1	2	0	0
18	Floor and spur base of conductor tip: at same level/ separated	0	0	0	1	1	0	0	0	1	1	1	1
19	Separation of conductor cap and pleats: large/ small	1	0	0	0	0	0	0	0	0	0	0	0
20	Cap of conductor: wide/ medium/ high	0	0	0	2	0	0	0	0	1	2	2	0
21	Cap of conductor: rounded/ pointed right/ flat	0	0	2	0	0	1	1	2	0	0	0	2
22	Tip of conductor twists to show underside?	0	1	1	1	1	1	1	1	1	1	1	1
23	Venter color: translucent/ dark	1	0	1	0	0	0	0	0	1	1	1	1
24	Venter pattern: plain/ median bar/ paired spots	1	1	2	1	1	1	1	0	0	0	1	1
25	Sternum color: translucent/ opaque	1	0	1	0	0	0	0	0	1	0	1	1
26	Orb webs built?	0	1	1	1	1	1	1	1	1	1	1	1
27	Tip of ♂ conductor projection: blunt/ pointed	0	0	0	0	1	1	1	1	1	1	1	1
28	Seminal receptacles: no swelling/swelling angled down/ angled up	0	2	0	2	0	2	2	2	1	1	2	2
29	Dorsum color: brown/ variable/ green	0	1	0	2	2	2	2	2	0	0	0	0
30	Tibial spines (lateral, medial, dorsal): 332/ 442/ 552	0	1	2	2	1	2	1	2	0	0	0	1

TABLE 1. Characters used for generating phylogeny. stel = *T. stelarobusta*; kau = *T. kauaiensis*; pil = *T. pilosa*; mac = *T. macracantha*; pol = *T. polychromata*; tant = *T. tantalus*; wak = *T. waikamoi*; brev = *T. brevignatha*; perr = *T. perreirai*; kam = *T. kamakou*; rest = *T. restricta*; quas = *T. quasimodo*.

there are three bright green species, one endemic to this volcano (*T. macracantha*), one shared with West Maui (*T. waikamoi*) and *T. brevignatha* shared with Hawaii Island. The East Maui species exhibit parapatric ranges, with only very narrow zones of overlap, and are more closely related to species on other islands rather than to each other,

DISCUSSION

Differentiation between species of the spiny-leg clade of Hawaiian *Tetragnatha* appears never to have occurred on the same mountain mass: in no situation are two sister species found on the same volcano, or even on the same island. This

phylogeny based on morphological characters therefore strongly suggests that strict geographic isolation (between islands only) is necessary for the initiation of species formation. Such isolation appears also to underlie speciation events in the Hawaiian *Drosophila* (Carson and Templeton, 1984). The phylogeny of the Hawaiian spiny-leg *Tetragnatha* also indicates that species colonize in a generally southerly direction, with the most ancestral taxa occupying the oldest island, Kauai. In addition, colonization of the most recent island (Hawaii) may be associated with ecological release: populations of each of the three species that have colonized Hawaii Island, *T. quasimodo*, *T. restricta* and *T. brevignatha*, occupy a broad

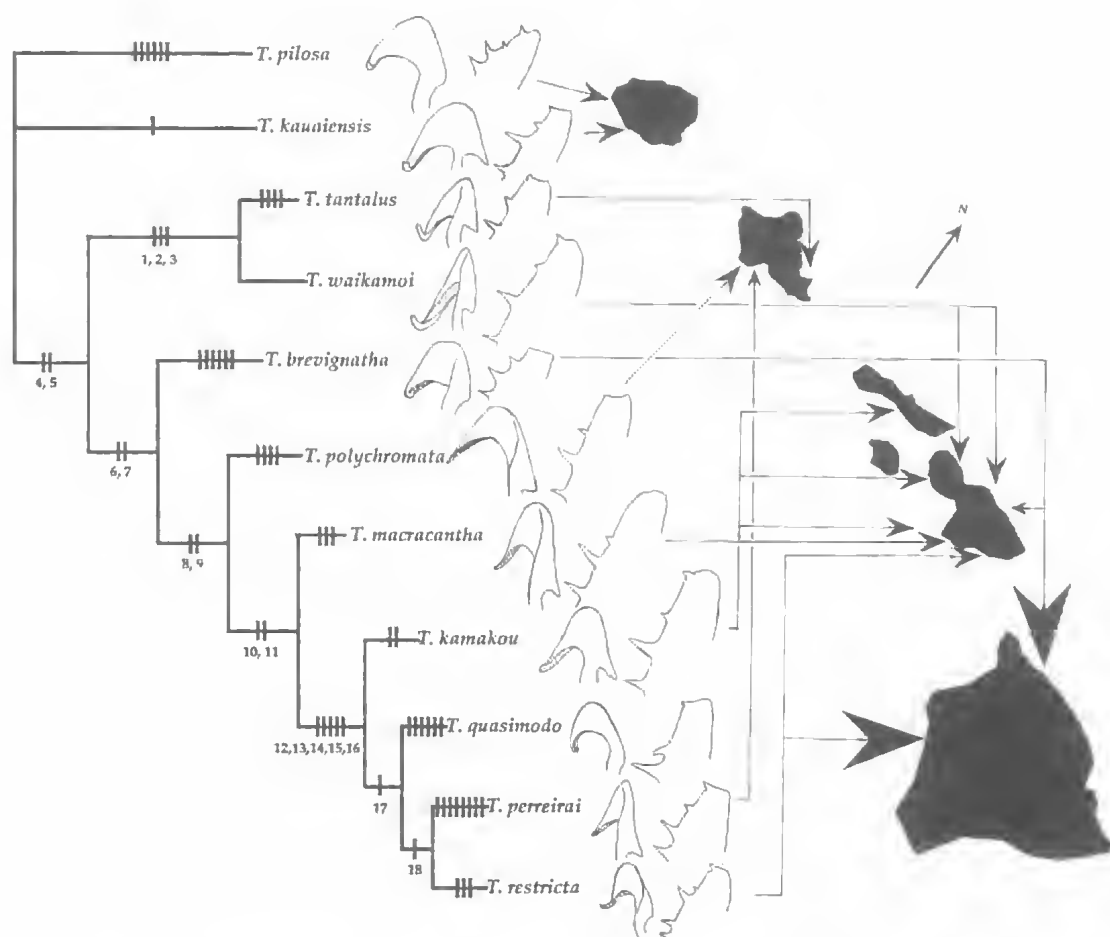


FIG. 2. Phylogeny of the Hawaiian spiny-leg *Tetragnatha* based on morphological characters. Explanations are given for characters defining each node; characters defining species are marked as bars. Sketches of the tip of the male conductor (left) and the upper surface of the apical portion of the male chelicera (right) are included for ease of comparison. Arrows point to the location of a species in the archipelago, with the size of an arrow tip being approximately proportional to the size of the distribution of a given species. Character changes defining each node are as follows. 1, Conductor terminal projection: short→long. 2, Conductor cap ridge: lateral→medial. 3, Conductor cap: rounded→pointed. 4, Conductor cap tip: blunt→pointed. 5, Colour: brown/variable→green. 6, First upper cheliceral tooth lost. 7, First lower cheliceral tooth lost. 8, First 2 lower margin cheliceral teeth→well separated. 9, Conductor backward projection at level→below cap. 10, Conductor cap: low→high. 11, Backward projection conductor spur→angled down. 12, Venter: pale→dark. 13, Abdomen colour: green→brown. 14, First dorsal cheliceral tooth→finger. 15, Cheliceral 'sl' tooth→closer to 'T'. 16, First 2 lower cheliceral teeth→closer. 17, Conductor backward projection hooked up→angled down. 18, Lower tooth row long→short.

range of habitat types. In particular, *T. brevigynatha* is found in almost every habitat type on Hawaii Island, whereas representatives of the species on East Maui are confined to a narrow band of mesic forest at middle elevation.

There are some distinct differences between the pattern of phylogeny I have generated here for the Hawaiian *Tetragnatha* and patterns suggested for

the Hawaiian *Drosophila*. The Hawaiian *Drosophila* generally demonstrate single volcano endemism, one species having its closest relatives on an adjacent volcano. In contrast, the phylogeny I have generated for the spiny-leg species of Hawaiian *Tetragnatha* suggests a non-uniform and disjunct pattern. Possible explanations for the *Tetragnatha* pattern may best be

ISLAND	HAWAII											MAUI						MO LA		OAHU			KA
VOLCANO	Mauna Loa						M. Kea		Kh	Hu	W	Haleakala					Ka	La	Wainaes	Ko	Wai		
	S	W	W	E	E	Saddle	E	E				N	N	E	E	W							
Elevation	1-2	0-1	1-2	0-1	1-2	0-1	1-2	0-1	1-2	1-2	1-2	0-1	1-2	0-1	1-2	1-2	1-2	1-2	0-1	1-2	0-1	1-2	
<i>tantalus</i>																					X		
<i>palychramata</i>																			X	X			
<i>brevignatha</i>		X	X		X		X	X	X	X			X										
<i>macracantha</i>												X		X	X								
<i>waikamai</i>											X		X	X	X								
<i>kuiensis</i>																					X		
<i>kamakou</i>											X		X		X								
<i>perreirai</i>																				X			
<i>pilosa</i>																					X		
<i>quasimoda</i>	X	X	X	X	X	X	X	X	X	X	X		X	X	X		X	X	X				

TABLE 2. *Tetragnatha* species collected at different sites (islands, volcanoes and elevations, x 100m) through the Hawaiian Islands. Islands: MO= Molokai; LA= Lanai; KA= Kauai. Volcanoes: M. Kea= Mauna Kea; Kh= Kohala; Hu = Hualalai; W= W. Maui; Ka= Kamakou; La= Lanaihale; Ko= Koolaus; Wai = Waialeale.

considered by viewing the Hawaiian archipelago as a series of evolutionary snapshots, with speciation starting on Hawaii Island and developing on East Maui. The three species on the recently formed Hawaii Island are likely to be relatively recent colonists that have expanded their range and habitat use. Such ecological release subsequent to colonization is considered an important step in initiating species divergence in Galapagos finches (Grant, 1986). However, the widespread species on Hawaii Island are remarkably homogeneous, and none are endemic to the island. It may be that Hawaii Island is too young for speciation to have occurred in the spiny-leg Hawaiian *Tetragnatha*. The situation suggests that considerable movement of individuals occurs within the island, and gene flow between islands has been sufficient to prevent speciation during the period of existence of Hawaii Island.

The adjacent older volcano of East Maui was once part of the island complex, 'Maui Nui' (comprising Molokai, Lanai, East and West Maui). This island was likely first invaded by *T. tantalus*. Males may be better colonists than females (Bishop, 1990), but spiderlings would also arrive, and eventually give rise to a population that would expand its range on that island. However, colonists would continue to arrive on Maui Nui, and, at least initially, the original colonists would not be reproductively isolated from the secondary colonists of the same species. It is also possible that, if the secondary colonists included closely related heterospecifics, hybridization might occur, as newly forming taxa tend to have poorly developed sexual discrimina-

tion (Kaneshiro, 1976, 1983; Carson *et al.*, 1989). Indeed, it is possible that both *T. macracantha* and *T. brevignatha* arose through hybridization, which may play an important element in the formation of species in general (Endler, 1989).

As sexual discrimination and ecological adaptation develop, invaders would presumably lose their ability to colonize an occupied land mass. The pattern of distribution of representatives of the spiny-leg clade on older islands suggests that closely related taxa cannot maintain coexistence on the same land mass unless they have undergone sufficient ecological divergence. The situation on East Maui may therefore represent an unstable state: ultimately, a single species will take over the land mass, as a result of introgression or competitive displacement.

The mechanism I have proposed for speciation among representatives of the spiny-leg Hawaiian *Tetragnatha* remains speculative. However, the repeated ecological release of newly forming taxa strongly suggests that ecological changes have played some role in initiating species divergence, as does the finding that two populations (Maui versus Hawaii) of an apparently diverging species (*T. brevignatha*) differ only in terms of their habitat occupation. I suggest that, unlike the Hawaiian *Drosophila* in which sexual selection has been heavily implicated in the speciation process (Kaneshiro, 1983; Kaneshiro and Giddings, 1987), ecological factors (range expansion, reinvasion, competition) may be more important among the spiny-leg species of Hawaiian *Tetragnatha*.

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